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# Spontaneous recovery of functional diversity and rarity of ground-living spiders shed light on the conservation importance of recent woodlands

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1 **Spontaneous recovery of functional diversity and rarity of ground-living**  
2 **spiders shed light on the conservation importance of recent woodlands**

3

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25 **Abstract**

26 Secondary (or recent) woodlands, whose development is favoured by massive farmland  
27 abandonment, are increasingly seen as promising habitats that limit losses of biodiversity and  
28 ecosystem processes. The importance of temporal forest continuity (i.e. the duration of an  
29 uninterrupted forest state) for conservation of the forest fauna has been demonstrated for  
30 several taxa, but its influence on functional diversity and conservation importance of  
31 communities remains unclear. We studied how temporal continuity can shape taxonomic and  
32 functional composition and structure of forest-ground spider communities at a regional scale.  
33 According to broad-scale ecological site characteristics, species composition and – to a lesser  
34 extent – trait distribution substantially diverged between ancient and recent forest sites. Yet,  
35 we found hardly any significant differences in functional  $\beta$ -diversity, community structure, or  
36 conservation importance between the two forest categories. The only difference was for  
37 functional originality, which quantifies the average functional uniqueness of species within an  
38 assemblage: spiders' communities of the ancient forests was more functionally original than  
39 those of the recent woodlands. Thus, in a conservation perspective, our study provides  
40 evidence that each forest harbours original species combinations, suggesting that each of them  
41 is irreplaceable, especially for ancient forests, which are functionally more original; however,  
42 recent woodlands have a high potential to spontaneously recover typical forest fauna  
43 communities with very similar structural and functional profiles to those of ancient forests.

44

45

46 **Keywords**

47 Arthropods; Farmland abandonment; Land use changes; Rewilding; Feral woodlands

48

## 49 **Introduction**

50 Land use change is considered as one of the major drivers of biodiversity changes in the  
51 terrestrial biosphere (Newbold et al. 2015). It can result in loss of both local and regional  
52 biodiversity (Sala 2000) or represent an opportunity for biological conservation through  
53 spontaneous rewilding (Pereira and Navarro 2015). Beyond modifications of species  
54 composition and structure of assemblages, these changes may affect ecosystem functioning  
55 (e.g. productivity, material cycling or resilience) by driving shifts of functional features of  
56 communities; e.g. by favouring the development of fast-growing plant species and thereby  
57 increasing ecosystem productivity (Allan et al. 2015). As a consequence, biodiversity  
58 conservation and related ecosystem processes are highly dependent on our understanding of  
59 the way historical and present land uses shape ecological communities. This is especially the  
60 case of mature ecosystems such as forest environments, which harbour high levels of  
61 biodiversity and numerous specialist species.

62 For centuries, regional species pools of woodlands have continuously been reshaped  
63 by successive periods of deforestation and reforestation (Kirby and Watkins 2015). These  
64 oscillations of the forest cover have brought about a profound dichotomy in forest landscapes,  
65 with coexistence of ancient forests and recent woodlands. In Western Europe, this trend  
66 increased in the last decades following massive abandonment of agricultural land resulting  
67 from socio-economical changes in developed countries (Renwick et al. 2013). Ancient forests  
68 are defined by the absence of a historical record of agricultural land use (and not as the  
69 absence of management) and have been continuously wooded for centuries (Hermy et al.  
70 1999). Recent woodlands result from spontaneous processes of ecosystem de-domestication  
71 (Hermy and Verheyen 2007); they have been described as "feral" and are considered as novel  
72 ecosystems by several authors (Hobbs et al. 2013). This categorisation is not established yet  
73 (Miller and Bestelmeyer 2016; Murcia et al. 2014); it mainly relies on the importance of land-

74 use legacies (e.g. soil condition) that can lead to major differences in community composition  
75 and diversity between ancient and recent forests (see reviews by Hermy and Verheyen 2007;  
76 Spake et al. 2015).

77 In recent decades, there has been a growing effort to improve our understanding of  
78 forest fauna – including invertebrate taxa – responses to farmland abandonment (Bowen et al.  
79 2007; Spake et al. 2015). In Europe, the key role of ancient forests for the conservation of  
80 arthropod communities has been demonstrated for carabid beetles (Assmann 1999; Desender  
81 et al. 1999; Goßner et al. 2008), saproxylic weevils (Buse 2011) and millipedes (Magura et al.  
82 2015). Thus, although significant recovery of entomofauna has been noted in secondary  
83 woodlands (Queiroz et al. 2014), temporal forest continuity admittedly strongly influences  
84 species composition and richness of certain taxonomic groups through dispersal and  
85 recruitment limitations (Bowen et al. 2007; Spake et al. 2015).

86 Beyond these taxonomic differences, the functional responses of arthropod communities  
87 to forest continuity are still poorly understood when trying to determine whether recent  
88 woodlands can play a significant role in recovering biodiversity losses. Yet, by accounting for  
89 ecological differences among species, functional diversity may improve our understanding of  
90 ecosystem processes and functioning, e.g. community assembly or resilience (Cadotte et al.  
91 2011). In this perspective, several indices have recently been developed to assess the  
92 functional structure and composition of ecological communities, such as functional richness,  
93 functional divergence, or functional redundancy (de Bello et al. 2007; Villéger et al. 2008).  
94 These indices complement taxonomic approaches by decomposing diversity into facets that  
95 provide insights into niche size and complementarity within communities (Pavoine and  
96 Bonsall 2011). Additionally, recent developments of trait-based ecology have demonstrated  
97 that other facets such as functional originality (related to uniqueness in trait combinations),  
98 specialisation (related to distinctiveness in trait combinations) and rarity (assessed using

99 species geographical rarity and trait rarity) were important to account for the ecology of  
100 outliers in conservation studies (Mouillot et al. 2013b; Violle et al. 2017): focusing on the  
101 conservation of functional diversity and rarity optimises biological feature preservation and  
102 decreases the probability of losing ecosystem functions (Leitão et al. 2016; Mouillot et al.  
103 2013a). To further unravel forest fauna functional responses to temporal forest continuity, we  
104 developed an innovative approach based on spider communities. Spiders are one of the main  
105 ground-living predator arthropods. Thus, this group represents an important determinant of  
106 ecosystem functioning because spiders hold a key trophic position and regulate the soil biota  
107 both bottom-up and top-down. Moreover, contrary to taxonomic groups strongly dependent  
108 on a particular habitat (e.g. saproxylic organisms in old-growth forests) that are absent from  
109 pioneer ecosystems, their great diversity and abundance in numerous ecosystems makes them  
110 an excellent indicator of the way community structure is gradually reshaped by environmental  
111 change (Marc et al. 1999). Spider abundance and distribution are likely to change during  
112 reforestation strongly depending on vegetation structure and several other factors such as  
113 associated microclimate and litter architecture (Pearce and Venier 2006; Gallé et al. 2017).  
114 Therefore, shifts in environmental conditions during reforestation are expected to lead to  
115 variation in the composition and structure of ground-living spider assemblages (Ziesche and  
116 Roth 2008).

117 We analysed taxonomic and functional  $\beta$ - and  $\alpha$ - diversity of ground spider assemblages  
118 in forest at a regional scale with three goals: (i) identify the main broad-scale factors that  
119 influence variations in the composition (so called  $\beta$ -diversity) of spider communities within a  
120 regional area; (ii) assess whether spider community structure (so called  $\alpha$ -diversity) differs in  
121 ancient and recent forests, and (iii) assess whether spider community conservation importance  
122 also differs, using a combination of complementary  $\alpha$ -diversity indices based on assemblage  
123 rarity and specialisation. We used a large regional spider database to perform, for the first

124 time to our knowledge, a comprehensive geographical assessment of taxonomic, structural,  
125 and functional comparisons of communities between ancient and recent forests at a broad  
126 regional scale.

127

## 128 **Materials and methods**

### 129 **Study sites and dataset**

130 We compiled data from a regional reference database including individual studies conducted  
131 in different environments in the Armorican Massif (western France) (see Leroy et al. (2013)  
132 for a presentation of the database). We extracted a subset of 56 spider assemblages sampled in  
133 forests from this database by applying a series of criteria (Fig. 1a). We selected only  
134 assemblages derived from plots of mesophilic oak-beech-dominated mature forest (for  
135 example, we avoided plantations and coniferous woodlands and young forests such as  
136 coppices), to limit the influence of environmental heterogeneity and stand maturity. These  
137 plots were homogeneous sets of ~ 1 ha corresponding to management units and were  
138 distributed in 16 sites across the regional area (Fig. 1, Online Resource 1). Then, we retained  
139 sites larger than 10 ha to avoid areas in which assemblages could be strongly influenced by  
140 edge effects. This selection resulted in 56 sites composed of one to six plots separated by 0.1  
141 Km to 2 Km (Online Resource 1). Within-site distances were always smaller than inter-site  
142 distances, which ranged from 5 Km to 200 Km. Then, we set apart spider communities of  
143 ancient forests from those of recent woodlands by checking the temporal forest continuity of  
144 each forest site using Cassini map layers (year 1790) and the Napoleonic cadastre (year 1847).  
145 These two historical land-use documents allowed for a precise spatialisation of ancient forests  
146 in France. We defined ancient forests as sites already forested in the middle of the 18<sup>th</sup>  
147 century, when the overall forested area was at its minimum over the French territory (Cateau  
148 et al. 2015). Hence, ancient forests are plots that have had an uninterrupted forest state for at

149 least 220 years. Here we assume that temporal forest continuity as the absence of a historical  
150 record of agricultural land use and not as the absence of management, such as logging (Hermý  
151 and Verheyen 2007). We defined recent woodlands as forests resulting from afforestation  
152 during the 20<sup>th</sup> century, i.e. no more than 120 years old. Thus, our dataset included 12 ancient  
153 forests (n plots=37) and 4 recent woodlands (n plots=19). Such an unbalanced design  
154 illustrates that even if farmland abandonment is an important phenomenon in Brittany, it has  
155 rarely led to the emergence of large, contiguous wooded sites. However, the recent woodlands  
156 were well distributed within study area: each of the four geographical sets of sites contained a  
157 recent woodland (Online Resource 1). Each of them are located less than 3 km from an  
158 ancient forest (at least a small patch). Finally, we filtered collections to retain only  
159 standardised sampling protocols based on pitfall traps and focused on forest-ground spider  
160 communities. In each plot – the experimental unit –, the local species pool was compiled from  
161 3 pitfall traps spaced 10 m apart and all situated at the center of the plot. Collections were  
162 carried out from April to June (a period corresponding to the peak of spider activity in the  
163 region) of 2013, or 2014, or 2015 (see details on sampling methods in Online Resource 2).  
164 Species abundance values were standardised according to the number of days a trap was  
165 active, to account for the effect of trap disturbance. The final dataset included 5,719 adult  
166 individuals belonging to 110 spider species collected in the 56 plots.

167

### 168 **Environmental variables**

169 We considered nine environmental variables to characterise biogeographical, climatic,  
170 historical, and broad-scale ecological conditions at the regional scale: geological substrate (4  
171 categories: Granite rock, Sandstone, Schist or Volcanic rock), temporal forest continuity (2  
172 categories: ancient or recent), site area (Ha), latitude, longitude, temperature maximum in  
173 2015 (degree Celsius), mean annual rainfall (mm), number of hours of solar radiation for the



174 1997-2006 period, and altitude (m). We compiled them from data from the French National  
175 Geographic Institute ([www.geoportail.fr](http://www.geoportail.fr)) and the French weather forecast institute  
176 ([www.meteofrance.fr](http://www.meteofrance.fr)).

177

## 178 **Data analyses**

### 179 *Sampling effort: site richness and completeness*

180 We first analysed the robustness of our dataset by assessing the completeness index composed  
181 of the observed richness divided by estimated species richness (Soberón et al. 2007). We  
182 calculated three richness estimators (Chao2, Jackknife 1, and Incidence Coverage-based  
183 Estimator (ICE)) commonly applied on similar datasets (Hortal et al. 2006; Soberón et al.  
184 2007). We calculated completeness indices for the whole dataset, for a subset composed of  
185 ancient forests and another composed of recent woodlands, and for each of the 16 sites.  
186 Richness estimators were computed with the “fossil” R package (Vavrek and Vavrek 2011).

187

### 188 *From life-history traits to functional distance between species of the regional pool*

189 We selected a set of five life-history traits available in the literature to describe the functional  
190 features of the 723 spider species recorded in the regional database. Seventy-eight species  
191 whose trait values were not available in the literature were excluded from our analyses. Traits  
192 were chosen to obtain a multidimensional representation of functional features of spiders  
193 describing the main facets of their ecology: body size (continuous: maximum size of females ;  
194 log-transformed to reach more symmetric distribution ; Roberts 1995), feeding guild (7  
195 categories: ambush hunters, ground hunters, other hunters, sheet web, space web, orb web,  
196 wandering web), daily activity (3 categories: diurnal, nocturnal, both) (Cardoso et al. 2011),  
197 phenology (4 categories: spring, summer, autumn-winter, eurychron) and stratum utilisation  
198 (2 categories: ground-dwellers, vegetation-dwellers) (Harvey et al. 2002). Body size

199 influences a wide range of ecological and physiological characteristics of a species (e.g.  
200 locomotion, space use, life history) and strongly affects resource use (Brose et al. 2006).  
201 Feeding guilds, phenology, stratum utilisation and daily activity are linked to resource  
202 partitioning among species and permits to analyse resource-use strategies across different  
203 sites.

204 To measure functional  $\alpha$ - and  $\beta$ -diversity, we used euclidean-space-based approaches  
205 which represent the extent of niche space exploited by communities by simultaneously  
206 accounting for several traits (Fig. 1b). We built a multidimensional functional space based on  
207 the trait values of all species retained for our analyses (i.e. 645 species including all 110  
208 species observed in our dataset of woodland communities; Online Resource 3). Because most  
209 traits were categorical, we performed a principal coordinates analysis (PCoA; with Cailliez's  
210 correction based on a Gower dissimilarity matrix computed on species traits (Villéger et al.  
211 2008). To find the best multidimensional space possible, we used the mean-squared deviation  
212 (mSD) criterion that measured how faithfully the initial functional distances (based on trait  
213 values) were represented in the final multidimensional PCoA-based space, as recommended  
214 by Maire et al. (2015). The lower the mean-squared deviation, the higher the quality of the  
215 functional space. We thus kept 4 dimensions for the functional space (mSD = 0.008). All  
216 functional indices were then calculated for both  $\alpha$ - and  $\beta$ -diversity within this functional space  
217 (Fig. 1c-d).

218

219 *Taxonomic and functional composition of communities: insight into overall  $\beta$ -diversity*  
220 *patterns*

221 To quantify plot-to-plot compositional variation *within* and *between* the two forest categories,  
222 we measured pairwise dissimilarities between each pair of plots (i.e. the 56 assemblages  
223 retained after selection from the global database; Fig. 1) with Jaccard's index for the

224 taxonomic facet and Jaccard-derived dissimilarities for the functional facet (Villéger et al.  
225 2013). Functional  $\beta$ -diversity is based on the calculation of the ratio between unshared  
226 functional space and the total functional space filled by communities in the multidimensional  
227 space (Villéger et al. 2013). In addition, we assessed the contribution of a strict turnover  
228 within taxonomic and functional  $\beta$ -diversity, following the frameworks of Baselga (2010) and  
229 Villéger et al. (2013), respectively. The turnover index was independent of differences in  
230 species richness (Leprieur and Oikonomou 2014), so we strictly focused on species and trait  
231 turnover in  $\beta$ -diversity changes.  $\beta$ -diversity metrics were calculated using the “betapart” R  
232 package (Baselga and Orme 2012).

233

#### 234 *Taxonomic and functional structures of communities: insight into $\alpha$ -diversity patterns*

235 Community structures were first investigated through three taxonomic diversity indices:  
236 species richness, species abundance and – to better understand the response of traditional  
237 taxonomic indices to temporal continuity – Pielou’s evenness (which measures the evenness  
238 of abundance distribution among species). All indices that include abundance were based on  
239 standardised abundance, i.e. a continuous variable (see Table 1). To assess the functional  
240 structure of each community, we computed multivariate indices of functional diversity that  
241 measure functional distances of species from the volume of convex hull intersections in the  
242 multidimensional space. Thus, for all 110 species listed in the global species-by-site matrix,  
243 species coordinates in the overall multidimensional space were extracted to measure two  
244 complementary facets of functional diversity for each assemblage (Fig. 1c): functional  
245 richness (FRic) and functional divergence (FDiv) (Villéger et al. 2008). Furthermore, we  
246 estimated the functional redundancy (FR) of each assemblage by using the framework of de  
247 Bello et al. (2007) which measures FR as the difference between species diversity and Rao’s  
248 quadratic entropy based on their functional dissimilarity (see Table 1 for metric details).

249 Finally, to quantify shifts in trait distribution, we also computed community-weighted  
250 mean trait values (CWM) and the proportion of presence-absence in each category for  
251 categorical traits, using the “FD” package in R (Laliberté et al. 2014).

252

253 *Taxonomic and functional conservation importance: insight into patterns of rarity,*  
254 *specialisation and originality of spider communities*

255 We used the entire regional reference database to compute conservation importance analyses;  
256 hence, the importance of each forest category was assessed with the regional species pool (i.e.  
257 the 645 species retained for our analyses; (Fig. 1d)). Concerning the taxonomic facet, we used  
258 the Index of Relative Rarity ( $I_{RR}$ ) of Leroy et al. (2012). The  $I_{RR}$  is the average rarity level of  
259 each species assemblage, based on species rarity weights. Rarity weights are calculated with  
260 regional occurrence data, so that rare species are species geographically rare in the entire  
261 region. We calculated rarity weights with a method that can be adjusted according to a user-  
262 chosen rarity cut-off point (Leroy et al. 2012; 2013). This method assigns rare species rarity  
263 weights that increase exponentially when their occurrence falls below the rarity cut-off point.  
264 To ensure that the chosen cut-off would be sufficient to distinguish rarity patterns among  
265 assemblages, we defined cut-offs following the guidelines of Leroy et al. 2012: the rarity cut-  
266 off was defined as the occurrence level at which the average proportion of rare species in  
267 local assemblages was 25% (see Discussion in Leroy et al. 2012). The  $I_{RR}$  of a species  
268 assemblage was calculated as the average rarity weight of all the species of the assemblage,  
269 and subsequently normalised between 0 and 1. We used the “rarity” package (Leroy 2016) for  
270 these analyses.

271 Concerning the functional facet, we first used the recent framework proposed by  
272 Violle et al. (2017) to measure the functional rarity (FRar) of each assemblage. At a regional

273 scale, this index is based on the two main components of species rarity (Violle et al. 2017),  
274 namely taxonomic restrictedness ( $R_i$ ; regional-scale characteristic of a geographically  
275 restricted species) and functional uniqueness ( $U_i$ ; regional-scale feature of a species  
276 possessing unique traits). We applied the additive framework that combines regional  
277 taxonomic restrictedness and functional uniqueness. Thus, FRar of species  $i$  was estimated as  
278 the addition of  $R_i$  and  $U_i$  for each species recorded in the regional dataset. Finally, FRar of  
279 species from woodland assemblages were summed and then divided by species richness so  
280 that the index depended on rare species proportions but not on species richness.

281 Finally, we completed the assessment of forest continuity for conservation by  
282 assessing functional specialisation (FSpe) and originality (FOri) of communities. We used two  
283 multidimensional indices implemented through the framework of Mouillot et al. (2013b),  
284 which assesses the functional features of each local community in view of the species pool;  
285 see Table 1 for metrics details).

286

### 287 *Statistical significance tests*

288 Given the dependent structures of the dataset, we systematically integrated random effects  
289 into models to provide unbiased statistical significance tests. The chosen model structures  
290 account for hierarchical and/or spatial structures of the sampling design and make it possible  
291 to effectively avoid potential biases due to pseudoreplication (Davies and Gray 2015).  
292 Therefore, in each model (whether  $\beta$ - or  $\alpha$ -diversity), we defined the spatial structure with  
293 *regional provinces* grouping nearby sites (see Online Resource 1) and the hierarchical  
294 structure (sampling plots nested within *study sites*) as random effects.

295 To analyse patterns of  $\beta$ -diversities, we applied permutational multivariate analysis of  
296 variance (PERMANOVAs) on dissimilarity matrices (i.e. on the previously calculated Jaccard  
297 index and Jaccard-derived dissimilarities) to check whether assemblages differed according to

298 sites ('site effect') and to temporal forest continuity ('ancientness effect'). Then, still based on  
299 the same taxonomic and functional dissimilarity matrices, we performed principal coordinate  
300 analyses (PCoA) to visualise  $\beta$ -diversities and highlight the structure of the species-by-site  
301 dataset (i.e. the 56 assemblages). Finally, to interpret PCoA patterns, the nine environmental  
302 variables were fitted onto ordinations. For each variable, we evaluated the significance of the  
303 explanatory power with a Monte-Carlo randomisation test (9,999 permutations), and the link  
304 strength with ordinations, using the squared correlation coefficient. For both PERMANOVAs  
305 and environmental interpretations of the PCoA, random effects were integrated by restricting  
306 permutations between *regional provinces* and between *sites* to account for the spatial and  
307 hierarchical structures of the dataset, respectively. These analyses were treated with the  
308 "vegan" and "permute" R packages (Oksanen et al. 2017; Simpson et al. 2016).

309 To analyse patterns of  $\alpha$ -diversity, we tested the means of each continuous metrics (i.e.  
310 FRic, FOr) in ancient *versus* recent woodlands with linear mixed-effect models (LMMs). For  
311 species richness, which is a discrete variable, we used generalised linear mixed-effect models  
312 (GLMMs). For all models, temporal forest continuity was defined as a fixed effect, and  
313 *regional provinces* and *sites* as random effects. We log-transformed values of standardised  
314 abundance,  $I_{RR}$ , FOr and FSpe to improve model fitness. We used the "lme4" package (Bates  
315 et al. 2015) for these analyses.

316

317 All data analyses were performed using R version 3.4.1 (R Core Team 2017).

318

## 319 **Results**

### 320 **Sampling effort: site richness and completeness**

321 On average,  $19.01 \pm 5.57$  (mean  $\pm$  sd) species were sampled per site, ranging from 13 to 47.

322 The mean value of the three selected completeness estimators for the overall dataset was

323 relatively high ( $0.83 \pm 0.04$ ), suggesting that the information extracted from the database gave  
324 us a fairly satisfactory picture of the species composition of the spider communities observed  
325 in the forest environments we studied (Online Resource 4). Out of the 16 sites, two (Rennes,  
326 Stangala) displayed low values (0.65 and 0.66, respectively), and four others had no estimable  
327 values because the number of samples was too low (Bois du Chap, Cranou, Menez, and  
328 Sœuvres).

329

### 330 **Regional patterns of taxonomic and functional dissimilarities**

331 Pairwise dissimilarities of spider assemblages were high and quite similar (they ranged from  
332 0.66 to 0.74 for the taxonomic facet and from 0.76 to 0.82 for the functional facet across the  
333 entire study area, *within* and also *between* the two forest categories (Table 2)). In each case,  
334 pairwise functional dissimilarities were greater than taxonomic ones. However, when  
335 variation in species richness was controlled by focusing on the contribution of turnover to  
336 pairwise dissimilarities, functional variations were systematically lower than taxonomic  
337 variations (from 0.40 to 0.46 and from 0.56 to 0.67, respectively).

338

### 339 **Sources of variation in taxonomic and functional dissimilarity**

340 PERMANOVA results highlighted significant differences in the taxonomic composition of  
341 spider communities across the 16 forest sites and between the two forest categories. The “site”  
342 factor explained more than half of overall variance in the regional area ( $R^2 = 0.518$ ;  $p = 0.001$ )  
343 whereas the “temporal forest continuity” factor explained around 1/10 ( $R^2 = 0.096$ ;  $p = 0.001$ ).  
344 PERMANOVAs applied to functional composition also highlighted significant differences  
345 across the 16 forest sites ( $R^2 = 0.38$ ;  $p = 0.001$ ). Differences were likewise significant between  
346 the two forest categories, but the part of the explained variance was very low ( $R^2 = 0.034$ ;  $p =$   
347 0.01).

348 Our analyses of the taxonomic facet showed a strong separation between spider  
349 communities of ancient and recent forests on the PCoA (Fig. 2). Regardless of their  
350 geographical position, the communities sampled in the recent woodlands were all more  
351 similar to one another than they were to their geographic neighbours from ancient forests; and  
352 the reverse was true for ancient forest communities (Fig. 2; Online Resource 1). Thus, when  
353 the influence of the temporal forest continuity was analysed through the fitting of  
354 environmental variables within the ordination space, it appeared as one of the main factors  
355 leading to the taxonomic compositional variation within the regional area ( $r^2 = 0.35$ ,  $p = 0.001$ ;  
356 Table 3). Additionally, PCoA revealed that the taxonomic composition was also strongly  
357 influenced by the geographical locations and climatic conditions of the sites: on the one hand,  
358 spider communities clearly and strongly differed according to altitude and latitude ( $r^2 = 0.58$   
359 and  $r^2 = 0.54$ , respectively; Fig. 2; Table 3); on the other hand, the composition of spider  
360 communities was also significantly (but more slightly) correlated with solar radiation and  
361 longitude ( $r^2 = 0.34$  and  $r^2 = 0.20$ , respectively; Fig. 2; Table 3). Among the other four  
362 variables, “area of sites”, “rainfall” and “geological substrate” also had an influence, but to a  
363 much lesser extent ( $r^2 < 0.15$ ), while “temperature” was not significant.

364 Our analyses of the functional facet suggest that spider communities of recent and  
365 ancient forests were not distinguishable on the PCoA (Fig. 2). Only longitude and temperature  
366 were significantly correlated with the ordination ( $r^2 = 0.18$ ;  $p = 0.01$  in both cases; Table 3).

367 The two-axis PCoA performed at the taxonomic level summarised 21% of the variance  
368 of the Jaccard dissimilarity matrix, but the pairwise distances plotted onto the ordination  
369 space were proportional to the observed ones (indicated by the fact that the cloud of points  
370 approximately followed a straight line; see Shepard diagram in Online Resource 6).  
371 Concerning the functional facet, the PCoA summarised a larger part of the variance (28%),  
372 but less accurately so (Online Resource 6).



### 373 **Community structure and conservation importance**

374 The mean values of all the metrics describing community structure at the taxonomic (species  
375 richness, standardised abundance, evenness) and functional (functional richness, divergence,  
376 redundancy) levels did not differ between ancient forests and recent woodlands (Wald's test;  
377  $p > 0.05$ ; Fig. 3; Online Resource 5). Similarly, the metrics describing taxonomic ( $I_{RR}$ ) and  
378 functional (FRar) rarity in the two forest environments did not differ, nor did functional  
379 specialisation (Wald's test;  $p > 0.05$ ). In contrast, average functional originality of ground-  
380 living spider communities was significantly higher in ancient forests than in recent woodlands  
381 (Wald's test = 12.9;  $p = 0.0003$ ) (Fig. 4; Online Resource 5).

382 Additionally, several mean trait distributions (assessed with CWMs) showed  
383 significant differences between ancient and recent forests (Fig. 5; Online Resource 5). Thus,  
384 mean body size, the proportion of species carrying out their life cycle in autumn/winter, and  
385 the proportion of various hunters (called *other hunters*) were significantly higher in the  
386 communities of ancient forests (Wald's test = 4.75;  $p = 0.03$ ); the proportion of ground  
387 hunters was marginally higher in the ancient forests (Wald's test = 3.6;  $p = 0.056$ ). On the  
388 other hand, there were significantly more orb-web and space-web spiders as well as more  
389 vegetation-dweller species in the recent woodlands than in the ancient forests (Wald's tests =  
390 4.3, 8.9, 16.9;  $p = 0.04, 0.003, < 0.0001$ , respectively); the proportion of species active both in  
391 the daytime and at night was marginally higher in the recent woodlands (Wald's test = 3.7;  $p$   
392 = 0.053). Nine out of the 16 investigated traits did not show any differences between the two  
393 forest categories.

394

### 395 **Discussion**

396 Based on the available data at a regional scale, our study provides new insights into the  
397 ecological specificity of ancient and recent forests by comparing taxonomic and functional  $\beta$ -

398 and  $\alpha$ -diversity of ground-living spider assemblages. We obtained three main findings. First,  
399 taxonomic and functional composition of spider communities greatly varied within the study  
400 area, with lower biotic homogeneity at a regional scale than we expected. Second, we  
401 observed significant differences in species composition and trait distribution between ancient  
402 and recent forests. On the other hand,  $\beta$ -diversity converged when the composition was  
403 characterised from a functional point of view (the extent of trait distribution, not their mean).  
404 Third, the community structure and conservation importance of the two forest categories did  
405 not reveal significant differences, except for functional originality.

406

#### 407 **Compositional specificity of forest sites within the regional area**

408 We found strong plot-to-plot variations ( $\beta$ -diversity) in taxonomic and functional composition  
409 within and between the forests (Jaccard dissimilarities  $> 0.7$ , Table 2). In addition, the relative  
410 part of strict functional turnover was lower than the taxonomic one (0.44 and 0.61,  
411 respectively; Table 2). This interesting finding suggests that species replacement did not  
412 systematically lead to a shift in functional composition and suggests probable trait redundancy  
413 in spider communities inhabiting forest environments in our region.

414         These compositional differences – especially taxonomic ones – were strongly linked to  
415 site identities (see PERMANOVA results). This result suggests that each forest site exhibited  
416 to some extent an original composition of ground-living spider communities, and, to a lesser  
417 extent, distinct combinations of life-history traits. Temporal forest continuity appeared as one  
418 of the major factors explaining taxonomic  $\beta$ -diversity among spider communities; this was  
419 especially represented by one of the two major axes of taxonomic compositional variation  
420 within the regional area (Fig. 2). In addition, other environmental characteristics of the sites  
421 (altitude, latitude, solar radiation, longitude) also significantly influenced global dissimilarity  
422 and represented the second major axis of taxonomic compositional variation. We thus found

423 that the main sources of taxonomic and – to a lesser extent – functional  $\beta$ -diversity were the  
424 geographical positions of the forests within the regional area, i.e. the longitudinal and  
425 latitudinal coordinates of the sites as well as their altitudes (Table 3). Combined with the other  
426 geographical differences in parameters such as rainfall, temperature, or solar radiation, the  
427 strong effects of these variables suggest a great influence of broad-scale climatic conditions  
428 on the regional  $\beta$ -diversity of forest spider communities. These results are consistent with our  
429 knowledge of niche properties of spiders that are conditioned by the interplay of a few abiotic  
430 factors strongly linked to climatic conditions, namely shading and moisture (Entling et al.  
431 2007).

432 A secondary significant source of taxonomic  $\beta$ -diversity was the geological substrate.  
433 Thus, although we restricted our investigations to one forest type (i.e. oak- and beech-  
434 dominated woodlands), this finding may suggest that our dataset included contrasting  
435 vegetation types and physiognomies linked to geological substrates and, as a corollary,  
436 distinct spider communities. Plant community composition indeed strongly influences  
437 arthropod assemblages, including predators, because of numerous causal factors (e.g.  
438 vegetation structure, predator-prey interactions, microclimatic conditions) that affect  
439 invertebrate distribution (Schaffers et al. 2008). The surface area of sites also captured a  
440 significant part of the variance of taxonomic dissimilarities, suggesting that site periphery  
441 influenced species composition. Landscape structure influences the composition of spider  
442 assemblages because it drives the availability of surrounding habitat sources (Öberg et al.  
443 2007) and edge habitats (Pearce et al. 2005). More specifically, smaller forest patches could  
444 be occupied by open-habitat specialist spiders absent in large forests because their high edge-  
445 to-area ratio favours an edge effect and individual moving (Gallé 2008).

446 Beyond these significant relationships between  $\beta$ -diversity and sites broad-scale  
447 ecological characteristics, a large part of overall taxonomic and functional  $\beta$ -diversity

448 remained unexplained (48% of total variance, see PERMANOVA results). A first explanation  
449 could be linked to fine-scale ecological parameters that we did not evaluate (e.g. see Pinzon et  
450 al. 2018), and which could lead to environmental heterogeneity of forest biota. Several factors  
451 can affect spider community composition, such as vegetation structure, litter architecture, or  
452 such as micro-climate, soil moisture, soil type, organic matter content, pH, fertility, as well as  
453 management practices (see Prieto-Benítez and Méndez 2011; Schaffers et al. 2008). A second  
454 explanation may arise from stochastic processes such as probabilistic colonisation (Mallis and  
455 Hurd 2005) or historical contingencies. The ranking and timing of species immigration during  
456 colonisation processes, known as priority effects, can also affect local occurrence and  
457 abundance and may generate various patterns of species composition (Fukami 2015). Finally,  
458 temporal fluctuations of the abundance of spider populations affect their detectability and may  
459 also influence the geographical patterns observed in species composition (Gossner et al.,  
460 2014). This could increase differences among communities when comparisons are based on  
461 results of pluri-annual field surveys. In this context, it would be interesting to complete our  
462 investigations by a study integrating a longer sampling period that would smooth out the  
463 potential phenological variations across sites.

464

465 **Trees do not make forests: major differences in taxonomic composition, and shifts in**  
466 **trait distribution between ancient and recent forests**

467 Our findings provide clear evidence that taxonomic composition of ground-living spider  
468 communities significantly differs between ancient and recent forests. Spider communities  
469 sampled in the same type of forest were more alike than spider communities sampled in  
470 different types of forest, regardless of their geographical positions. On the other hand, we did  
471 not find any difference in functional  $\beta$ -diversity between forest categories; but we found  
472 significant differences in the life-history trait distributions (Fig. 2; Fig. 5). Altogether, these

473 results are consistent with our expectations that forest continuity leads to ecological  
474 differences between woodlands and in turn generates various compositional patterns by  
475 affecting spider niche properties. It is now well known that recent woodlands differ  
476 ecologically from ancient forests (see the review by Hermy and Verheyen 2007). These  
477 ecological differences are mainly due to agricultural legacies that may sometimes strongly  
478 and lastingly impact soil properties such as pH, organic matter, carbon/nitrogen/phosphate  
479 contents, and in turn pedofauna and vegetation composition (Dupouey et al. 2002; Flinn and  
480 Marks 2007). Changes in soil physicochemical properties and associated food webs (i.e.  
481 brown and green food webs) in turn affect upper trophic levels such as arthropod predators by  
482 influencing local microclimates, habitat structure or prey availability (Pearce and Venier  
483 2006; Ziesche and Roth 2008). As a consequence, given the weak dispersal abilities and the  
484 strong association of forest specialist arthropods to micro-habitats and physical conditions of  
485 woodlands (i.e. moisture and shadow), their potential establishment in recent re-growth  
486 forests needs time (Bowen et al. 2007; Spake et al. 2015). This greater proportion of  
487 specialised species (occupying a restricted niche) in ancient forests is especially illustrated in  
488 terms of traits by the overrepresentation of species that carry out their life cycles in  
489 autumn/winter as compared to recent woodlands (Fig. 5). This was the case for *Centromerus*  
490 *brevipalpus* or *Hahnia ononidum*, two strictly forest-dwelling spiders (Online Resource 3,  
491 Online Resource 7). Otherwise, these compositional differences between the two types of  
492 forests may also result from the temporary maintenance of species associated to earlier  
493 successional stages in recent woodlands. We indeed observed that values or categories of life-  
494 history traits that can favour the colonisation of new habitats were better represented in recent  
495 forests than in ancient forests. These traits included a small size, generalist traits such as large  
496 daily activity (both diurnal and nocturnal), or membership in hunting guilds primarily using  
497 webs (Fig. 5), because such traits make species more prone to dispersal (ballooning) and less

498 dependent on the soil biota (Nentwig 1986; Gobbi 2017). This is typically the case of the  
499 Linyphiidae family. Moreover, temporal continuity could interact with stand maturity and  
500 cause variations in species composition (Janssen et al. 2017). Thus, although we carefully  
501 selected forest plots with similar maturity, a few compositional differences may have been  
502 related to structural attributes such as dead-wood material or litter complexity, which also  
503 influence spider distribution (Buddle 2001; Bultman et al. 1982). This is the case for some  
504 species more specifically found under dead wood stumps or forest floor stones (e.g. the large  
505 cribellate spider *Amaurobius similis* or the sheet-weaving spider with tubular retreat  
506 *Eritagena picta*). Future investigations should account for this distinction and refine our  
507 understanding of the influence of forest continuity on spider community structuring. Finally,  
508 some of these compositional differences may not be linked to deterministic factors: as  
509 predicted by the theory of community assembly, stochastic forces such as historical  
510 contingency (e.g. priority effects) or neutral processes such as dispersal and ecological drift  
511 may interact with environmental filtering and biotic interactions to shape communities and  
512 partly result in unpredictable assemblages (Chase 2003; Fukami 2015).

513

#### 514 **Trees make forests: convergence of community structures between ancient and recent** 515 **forests**

516 Despite differences in taxonomic composition and trait distribution, functional  $\beta$ -diversity,  
517 community structure and conservation importance were highly similar in the two forest  
518 categories. A first consequence is that the degrees of functionality ensured by spider  
519 communities in both ancient and recent forests seemed unchanged: functional richness  
520 suggests that niche sizes (i.e. the volumes of functional space) exploited by spider  
521 communities were identical (Fig. 3a-b). Furthermore, the consistency of abundance values  
522 and the high values of Pielou's evenness index suggest that ecological niches were exploited

523 with the same intensity, i.e. species shared available resources similarly in ancient and recent  
524 forests (Fig. 3c-e). The lack of differences in functional divergence shows that the degrees of  
525 niche differentiation in the communities were also similar (Fig. 3d) (Mouchet et al. 2010;  
526 Villéger et al. 2008). Additionally, the same levels of functional redundancy suggest that  
527 spider species performed similar functions in the two forest categories and were therefore  
528 interchangeable, with little impact on ecosystem processes (Fig. 3f) (Fonseca and Ganade  
529 2001). The low  $I_{RR}$  values revealed that the communities of the ancient and recent forests  
530 were dominated by species otherwise widespread in western France. Moreover, ancient  
531 forests did not harbour communities with rarer functional features than recent woodlands  
532 relatively to the regional area (Fig. 4a-b). Similarly, functional specialisation of forest spider  
533 communities did not differ over time, suggesting similar widths of the ecological niches  
534 exploited by spiders in all forest environments (Fig. 4d). Previous studies investigating  
535 biodiversity responses to farmland abandonment found that fauna taxonomic structure in  
536 secondary forests could rapidly resemble fauna taxonomic structure of ancient forests (Bowen  
537 et al. 2007; Spake et al. 2015). More precisely, no difference in  $\alpha$ -diversity between ancient  
538 and recent forests was found in communities of ground-living beetles (Assmann 1999) and  
539 spiders (Hurd and Fagan 1992) in temperate ecosystems. By highlighting similar trends with  
540 functional metrics, our results are in line with research showing that recent woodlands can  
541 spontaneously recover forest fauna weakly impeded by dispersal constraints, including many  
542 arthropod groups (Nordén et al. 2014; Queiroz et al. 2014). Finally, these results raise the  
543 important question of which conditions generate such rapid and spontaneous recovery of  
544 structures of ecological communities. Can these processes also be observed after the  
545 abandonment of agrosystems intensively exploited during the 20<sup>th</sup> century?

546 In contrast with these similarities between the two forest categories, we evidenced that  
547 ancient forests harboured functionally more original assemblages (Fig. 4c). A first potential

548 consequence is that ancient forests tend to harbour on average more functionally original  
549 species than recent woodlands do. In other words, species of ancient forests seem to be  
550 isolated within the functional space of the regional species pool. Among these species, several  
551 are known to be specific to habitat conditions more frequently found in ancient forests. For  
552 example, *Neon reticulatus* or *Saloca diceros* are two small litter-hunter specialist species  
553 generally associated with a dense leaf litter, exhibiting one of the most important values of  
554 functional originality, and only recorded in ancient forests (Online Resource 7a; Online  
555 Resource 3). Yet, there were also other species exclusively present in recent woodlands which  
556 showed high degrees of functional originality as well as analogous functional features to those  
557 exclusively present in ancient forests. For example, *Nerienne clathara* and *Linyphia hortensis*  
558 are two small sheet web linyphiidae observed exclusively in ancient forests and recent  
559 woodlands, respectively (Online Resource 7a; Online Resource 3). This result, combined with  
560 the fact that exclusive species are rare (Online Resource 7a), suggests that differences in  
561 species composition were not the only parameter explaining the mean differences in FOr<sub>i</sub>  
562 between the two forest categories. The higher FOr<sub>i</sub> of the spider communities of ancient  
563 forests likely also resulted from the greater representation (in terms of abundance) of  
564 functionally distinct species (e.g. forest specialists such as *Apostenus fuscus* or forest  
565 generalists such as *Pardosa saltans*; Online Resource 7a). Overall, whether in terms of  
566 species distribution or abundance, the most original forest spiders appear to be favoured in  
567 ancient forests, either because temporal continuity allows for the maintenance of populations  
568 over time, or because habitat conditions are better suited to their biological cycles. The fact  
569 that functional original spiders might be favoured in ancient forests is an interesting finding  
570 because it provides functional perspectives to previous works highlighting the importance of  
571 ancient forests to preserve highly stenoecous and relict arthropod species (Assmann, 1999;  
572 Buse, 2012).



**573 Study limitations**

574 Despite our efforts to improve the reliability of our dataset and the robustness of the analyses,  
575 our results should be interpreted considering the methodological limitations inherent to large  
576 datasets compiling different individual studies. Our main limitation lies in the fact that our  
577 design was unbalanced, with a larger number of plots sampled in ancient forests than in recent  
578 woodlands (n=37 vs. n=19). This imbalance was reflected in the lower global completeness  
579 value of recent woodlands, suggesting that these communities were sampled less accurately,  
580 even though two of the three estimators had similar values to those of ancient forests (Online  
581 Resource 4). In addition, most sites, whether ancient or recent, had relatively high  
582 completeness ( $> 0.75$ ). Nevertheless, this imbalance may have influenced both metrics related  
583 to geographic rarity ( $I_{RR}$ , FRar) because of a greater probability to detect rare species in  
584 ancient forests than in recent woodlands. However, this bias seemed to have little influence on  
585 our results: spider communities of ancient forests did not show higher values for  $I_{RR}$  or FRar  
586 (Fig. 4a-b), and their variances were homogeneous between the two forest categories ( $F$  test =  
587 1.66, 1.87;  $p = 0.25, 0.16$ , respectively;  $df_{num.} = 36, df_{den.} = 18$ ). These results suggest that, even  
588 with fewer pitfall traps, the distribution of these rarity values in the recent woodlands was  
589 similar to that of ancient forests. However, we consider our study as a first approach to  
590 examine the response of forest spider assemblages to farmland abandonment. This first  
591 approach is paving the way for future works based on more exhaustive data (both in terms of  
592 time and space), which will also account for fine-scale ecological parameters (e.g. abiotic soil  
593 conditions) and finer life-history traits, and complete our results. Overall, we feel that a  
594 collective research effort focusing on spontaneous rewilding would be welcome to assess to  
595 what extent and under which conditions recent afforestation may significantly contribute to  
596 the conservation of forest arthropods.

597

598 **Concluding remarks**

599 The present study shows that, combined with broad-scale ecological factors, temporal  
600 continuity contributes to generate various assemblages among forest sites. In a conservation  
601 perspective, this is an interesting result because it demonstrates that each forest, whether  
602 ancient or recent, is not equivalent and contributes to regional biodiversity. Thus, our results  
603 suggest that ground-living spider communities of ancient forests are irreplaceable because of  
604 their compositional uniqueness and high functional originality. However, by showing that  
605 communities with structural and functional profiles very similar to those of ancient forests can  
606 be recovered within a century, our results also highlight the promising conservation role  
607 possibly played by recent woodlands in times of global land-use changes.

608

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803 **Figures captions**

804 **Fig. 1** Overview of the step-by-step analytical framework (see Materials and Methods for  
805 details).

806

807 **Fig. 2** Ordination of the taxonomic and functional compositions of spider assemblages by  
808 principal coordinate analyse (PCoA) for the 56 assemblages (37 ancient forests and 19 recent  
809 woodlands). Overlap between spider communities of ancient forests (turquoise) and recent  
810 woodlands (red) is illustrated with one- (top and right of each graph) and two-dimensional  
811 kernel density (outer hull for 75%). The direction and the strength of the continuous  
812 environmental variables are represented by black arrows in each ordination (only significant  
813 variables; see Table 3). The strength of each variable is shown by the length of the arrow that  
814 is proportional to the correlation with ordination. The four symbols show the four identified  
815 groups of nearby sites (Online Resource 1).

816

817 **Fig. 3** Structure, taxonomic and functional  $\alpha$ -diversity of spider communities in ancient  
818 forests (n=37) and recent woodlands (n=19). Graphs show boxplots and means  $\pm$  standard  
819 errors. See methods for further details on the calculation of these indices.

820

821 **Fig. 4** Composite view of conservation value of spider' communities of ancient forests and  
822 recent woodlands combining taxonomic indicators (a) and functional metrics (b,c,d). Graphs  
823 show both boxplots and mean  $\pm$  standard errors. See methods for further details on the  
824 calculation of these indices.



825 **Fig. 5** Community-weighted mean (CWM) body size and proportion of presence-absence in  
826 each category for categorical traits of spider communities in ancient forests (n=37) and recent  
827 woodlands (n=19). Graphs show boxplots and means  $\pm$  standard errors. CWMs between the  
828 two forest categories were analysed with LMMs, except “Daily activity: Both”, ”Guild: Orb  
829 web” and ”Guild: Other hunters”, whose equivariance hypotheses were not validated and for  
830 which we performed GLMMs using Penalised Quasi-Likelihood (PQL).

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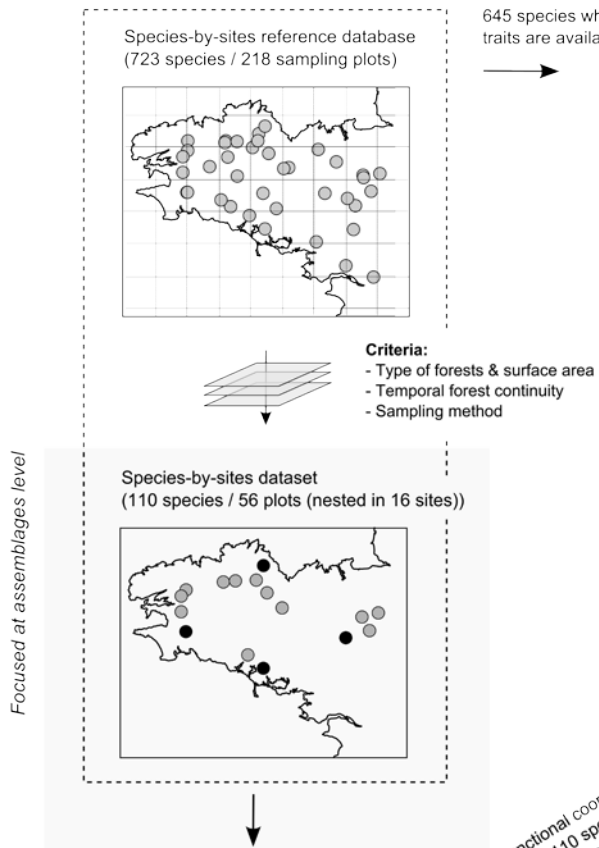
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851 **Figures**

852 Figure 1

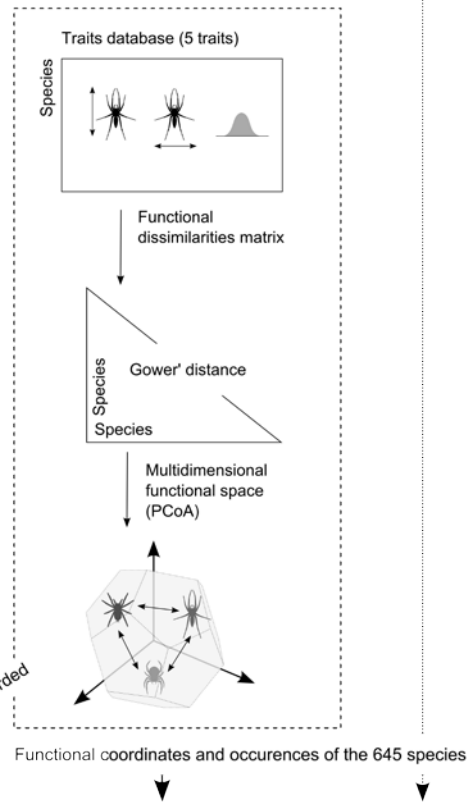
853 **Step 1 : Selection & preparation of the dataset**

854 (a) Selection of species-by-sites dataset



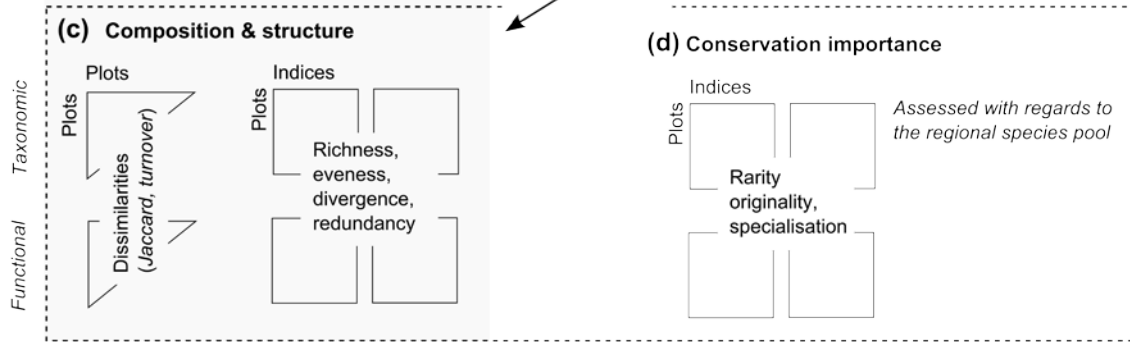
645 species whose traits are available

855 (b) Functional distance between species

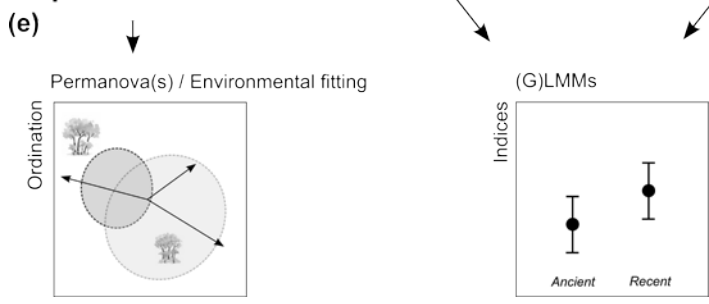


Functional coordinates of the 110 species recorded in the studied plots

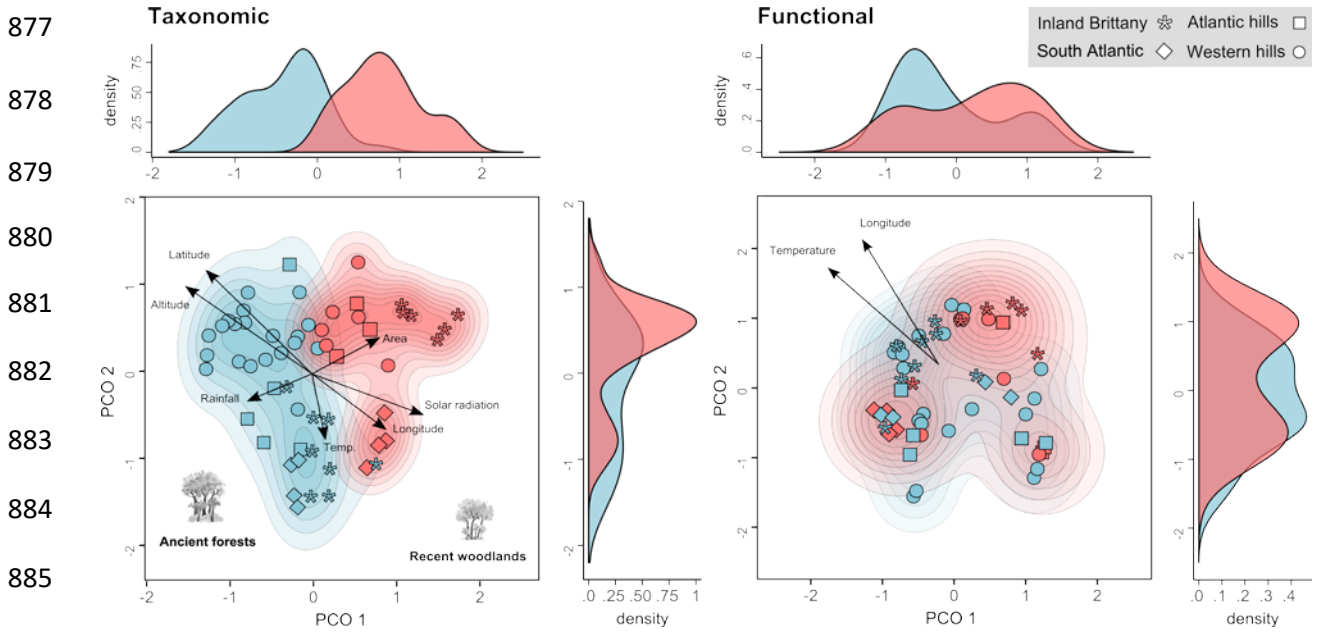
866 **Step 2 : Calculation of the indices**



872 **Step 3 : Statistical treatments**



876 Figure 2



903 Figure 3

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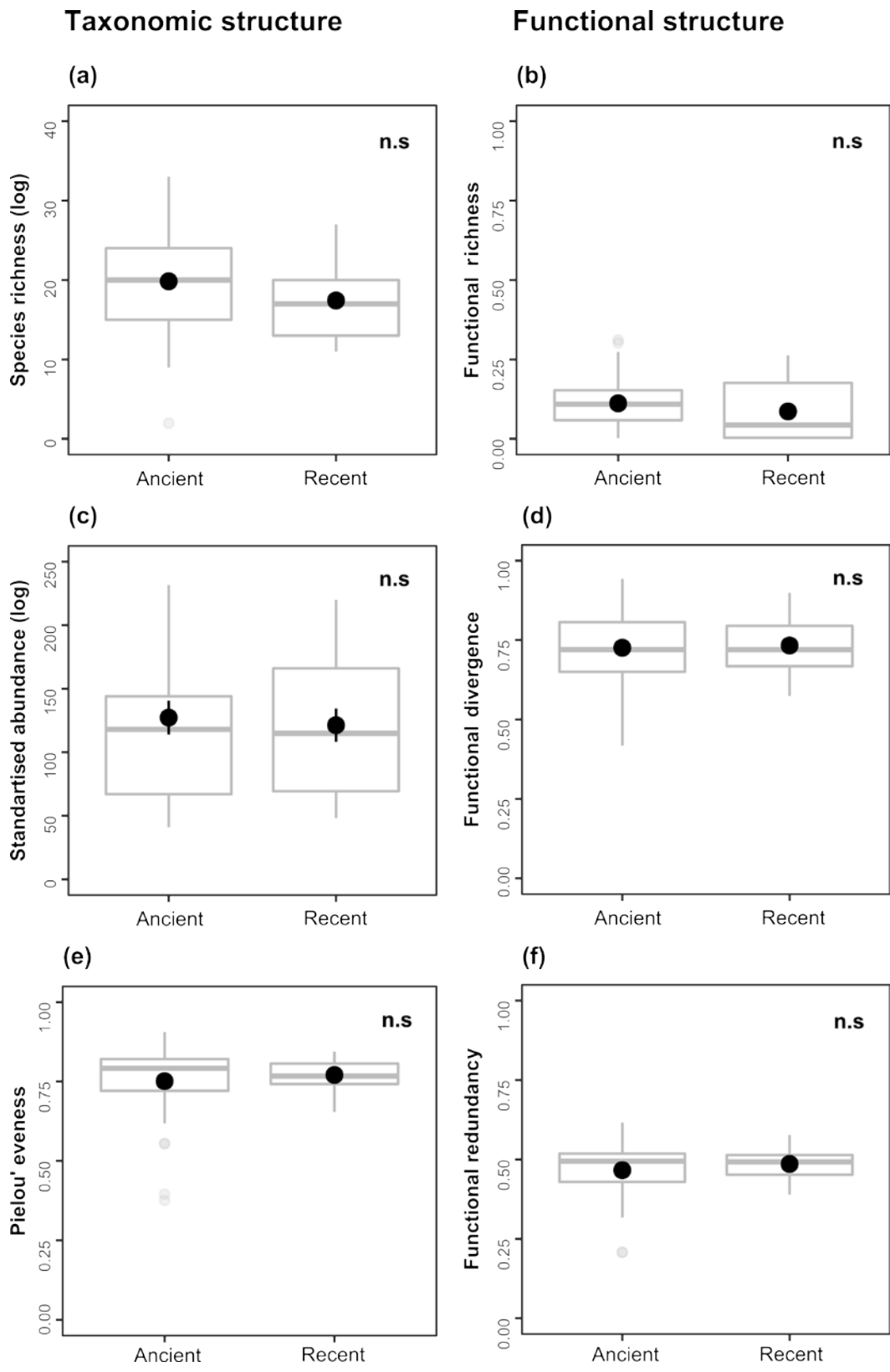
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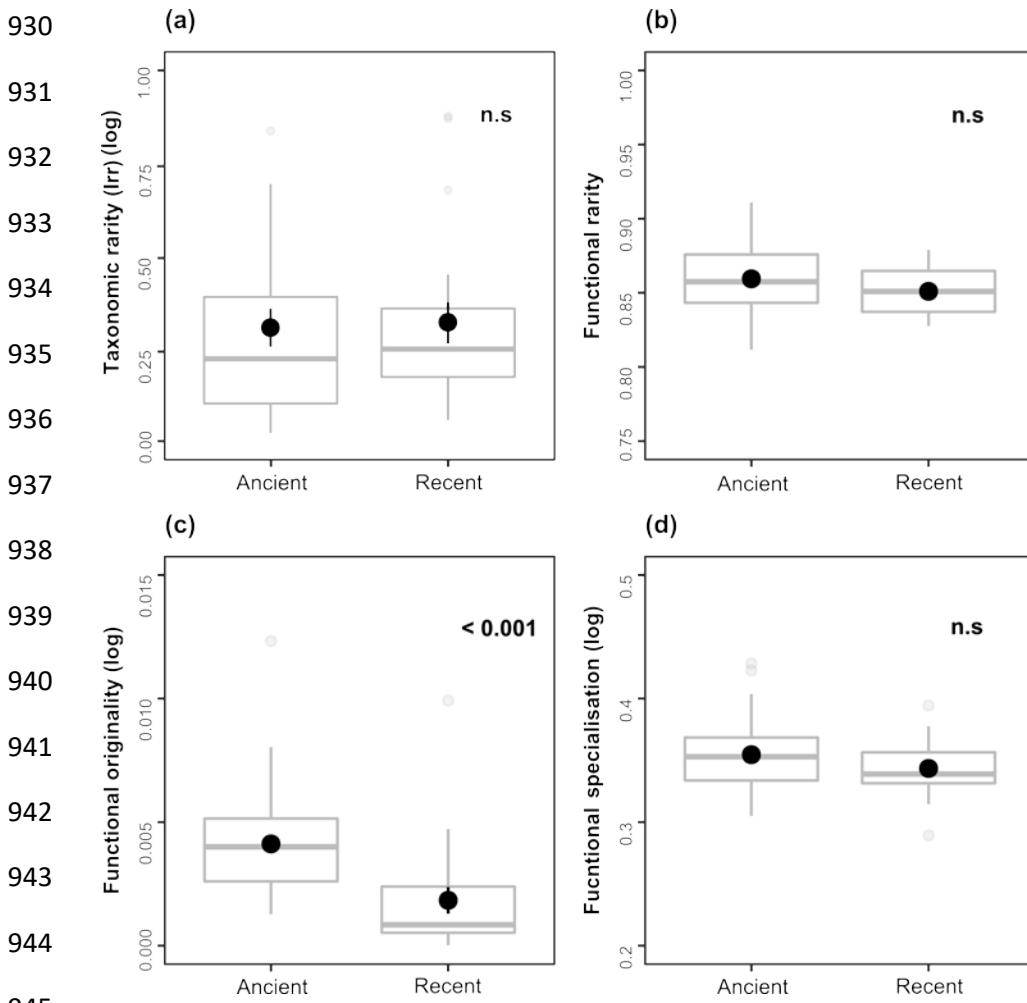
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929 Figure 4



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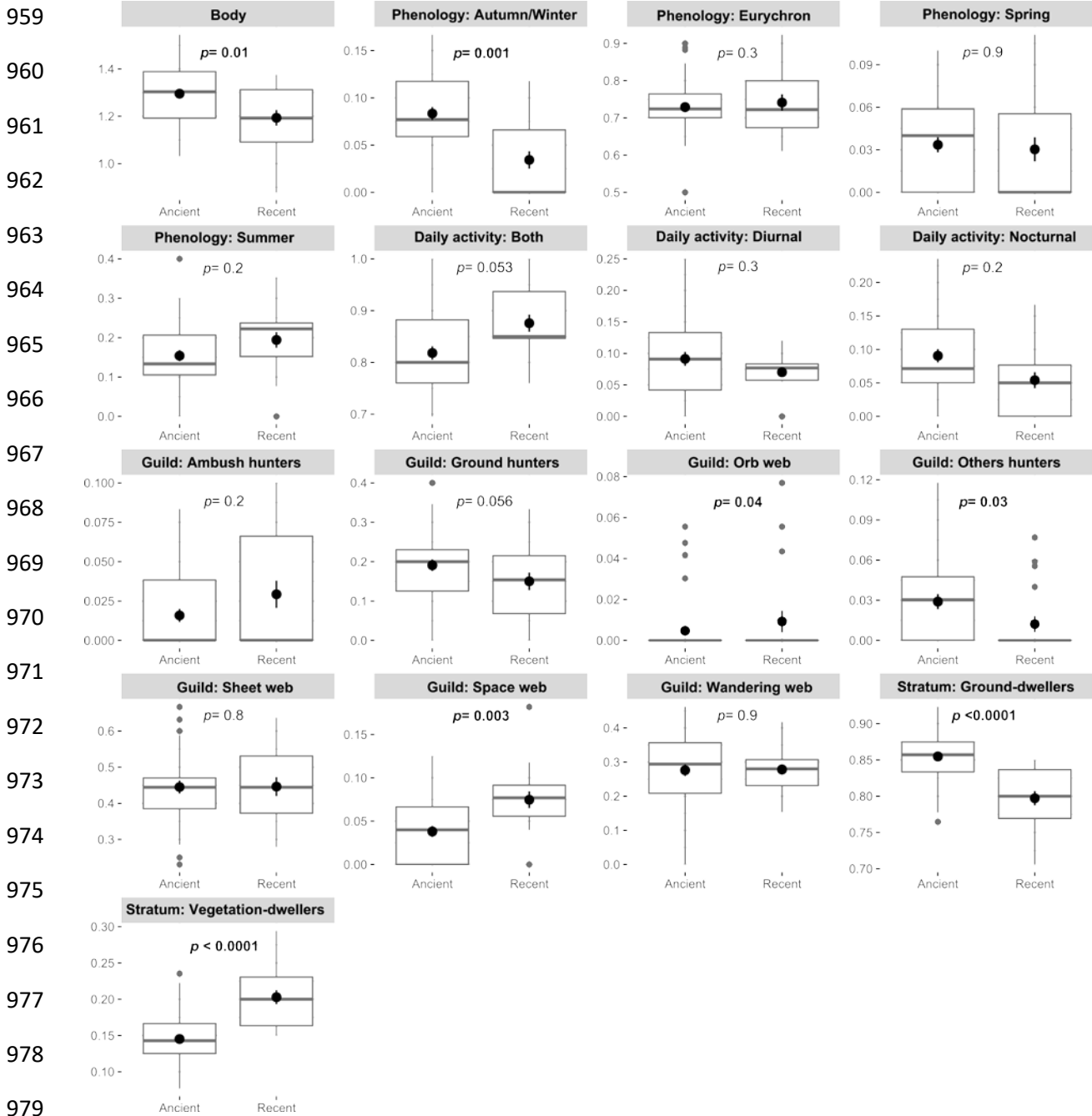
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957 Figure 5

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985 **Tables**

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987 **Table 1** Overview of the functional diversity indices used in the study at the  $\alpha$ -level. While  
 988 the first three indices analysed functional structure in each local community, FOr and FSpe  
 989 were measured from the whole pool, i.e. the 645 species included in the functional space.

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FD Component	Index	Measurement type	Weighted abundance	Influence of richness
<b>Local communities</b>				
Functional richness	FRic	the volume of multidimensional space occupied by all species in a community within a functional space	No	Yes
Functional divergence	FDiv	the proportion of total abundance supported by species with the most extreme trait values within a community	Yes	No
Functional redundancy	FR	difference between species diversity and Rao's quadratic entropy based on their functional dissimilarity	Yes	Yes
<b>Whole regional pool</b>				
Functional specialisation	FSpe	the mean distance of a species from the rest of the species pool in a functional space	Yes	No
Functional originality	FOr	the isolation of a species in the functional space occupied by a given community	Yes	No

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996 **Table 2** Summary of taxonomic and functional pairwise dissimilarities (Jaccard's index and  
 997 Jaccard-derived dissimilarities) (i) within overall plots, (ii) within ancient and recent forests,  
 998 (iii) between ancient and recent forests, and contribution of the turnover to each combination  
 999 of pairwise dissimilarities. Values are mean  $\pm$  standard deviation with confidence interval at  
 1000 95% in brackets.

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	Taxonomic	Functional
<b>Plot-to-plot variation</b>		
Overall forests	0.71 $\pm$ 0.09 [0.70 - 0.71]	0.79 $\pm$ 0.17 [0.78 - 0.80]
Contribution of turnover	0.61 $\pm$ 0.13 [0.61 - 0.62]	0.44 $\pm$ 0.27 [0.43 - 0.46]
Ancient forests	0.68 $\pm$ 0.09 [0.68 - 0.69]	0.76 $\pm$ 0.19 [0.74 - 0.77]
Contribution of turnover	0.58 $\pm$ 0.13 [0.57 - 0.59]	0.46 $\pm$ 0.25 [0.44 - 0.48]
Recent woodlands	0.66 $\pm$ 0.10 [0.65 - 0.68]	0.82 $\pm$ 0.16 [0.80 - 0.85]
Contribution of turnover	0.56 $\pm$ 0.14 [0.54 - 0.58]	0.40 $\pm$ 0.26 [0.36 - 0.43]
<b><math>\beta</math>-diversity between ancient and recent forests</b>		
Overall ancient vs. recent	0.74 $\pm$ 0.8 [0.73 - 0.74]	0.81 $\pm$ 0.16 [0.80 - 0.82]
Contribution of turnover	0.67 $\pm$ 0.12 [0.65 - 0.67]	0.43 $\pm$ 0.29 [0.41 - 0.46]

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1011 **Table 3** Pearson's correlation coefficients of the nine environmental variables based on PCoA  
 1012 ordination (see Fig. 2);  $r^2$  is the coefficient of determination and describes the goodness of fit,  
 1013  $p$  refers to the significance of the correlation between the gradient and the PCoA scores, based  
 1014 on a random permutation ( $n=9,999$ ). \*  $p \leq 0.05$ ; \*\*  $p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ .

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Environmental variables	Taxonomic		Functional	
	$r^2$	$p$	$r^2$	$p$
Altitude	0.58	***	0.01	n.s.
Area of sites	0.14	*	0.11	n.s.
Latitude	0.54	***	0.03	n.s.
Longitude	0.20	**	0.18	**
Rainfall <sub>1997-2006</sub>	0.12	*	0.02	n.s.
Temperature maximum <sub>2015</sub>	0.11	n.s.	0.18	**
Solar radiation <sub>1997-2006</sub>	0.34	***	0.01	n.s.
Geological substrate	0.14	***	0.11	n.s.
Temporal forest continuity	0.35	***	0.04	n.s.

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1025 **SUPPLEMENTARY MATERIAL**

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1028 **Title:** Spontaneous recovery of functional diversity and rarity of ground-living spiders shed  
1029 light on the conservation importance of recent woodlands

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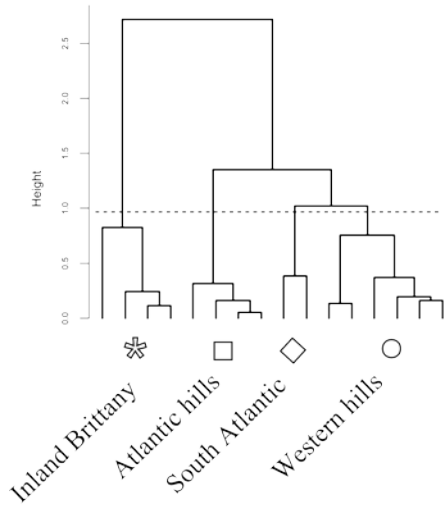
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1050 **Online Resource 1**

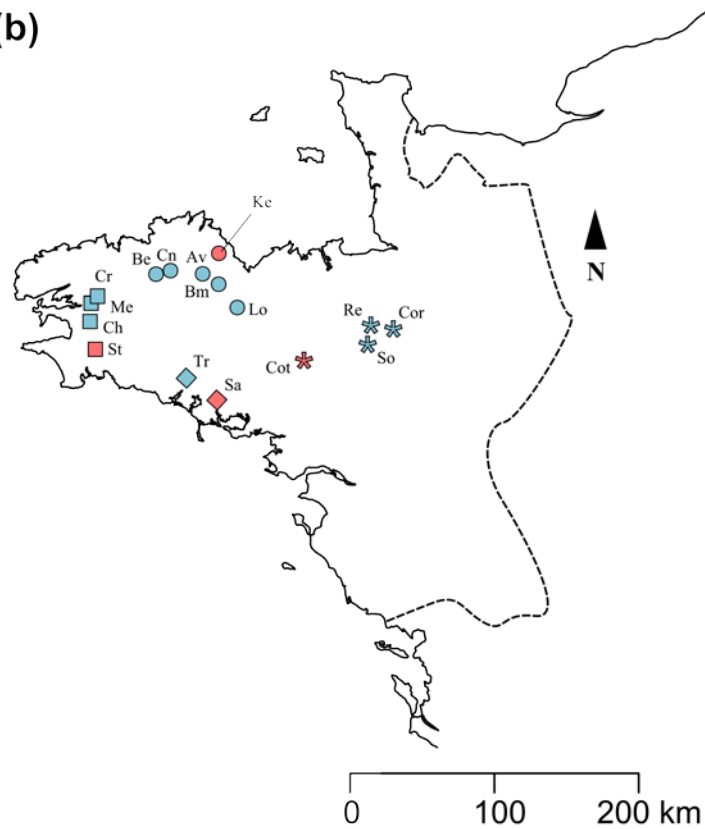
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(a)



(b)



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Spatial arrangement of the sampling design of the 16 study sites in the west of France. (a) Classification of each site based on their geographic positions (X and Y coordinates) (Euclidean distance, complete method); 4 groups of nearby sites were defined. (b) Map of the 16 study sites in the study region. See the table below for details of environmental features of each site and the specific sample design. Ancient forests are shown in turquoise, and recent woodlands in red.

1077 Summarised description of the forest sites according to the variables assessed at the site scale.

Sites	Abbreviation	No of plots	Geological substrate	Area (ha)	Altitude (m)	Sampling year
Avaugour	Av	6	Granite rock	1100	169	2013
Beaumanoir	Bm	3	Volcanic rock	300	214	2014
Beffou	Be	5	Volcanic rock	630	248	2014
Bois du Chap	Ch	2	Sandstone	40	91	2014
Coat-an-noz	Cn	3	Volcanic rock	1900	215	2014
Coetquidan	Cot	6	Sandstone	4000	97	2015
Corbières	Cor	3	Sandstone	630	101	2014
Cranou	Cr	2	Sandstone	1300	206	2014
Kério	Ke	6	Volcanic rock	200	94	2013
Lorges	Lo	3	Schist	2000	215	2014
Menez	Me	1	Sandstone	10	310	2014
Rennes	Re	3	Schist	3000	58	2014
Sal	Sa	4	Granite rock	52	32	2014
Soeuvres	So	2	Schist	115	54	2014
Stangala	St	3	Granite rock	57	59	2014
Tremelin	Tr	4	Granite rock	144	72	2014

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1086 **Online Resource 2**

1087 **Arthropod sampling**

1088 In each plot, three pitfall traps consisting of polypropylene cups (10 cm diameter, 17 cm deep)  
1089 with preservative solution (300 g.l<sup>-1</sup> of NaCl) (Spence and Niemela 1994), were placed at the  
1090 middle of the plots and spaced out 10 m apart along a 20-m transect. This distance was  
1091 considered to be the minimum distance to avoid interference between traps (Topping and  
1092 Sunderland 1992). Trap size and type were selected based on Lange et al. (2011) to optimise  
1093 arthropod sampling and limit the risk of trapping vertebrates involuntarily.

1094 The 168 traps (56 plots x 3 traps) were collected fortnightly from April to June of 2013, or  
1095 2014, or 2015, and stored in 70% ethylalcohol. Only adults were considered for the studies.

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1097 Lange M, Gossner MM, Weissr WW (2011) Effect of pitfall trap type and diameter on  
1098 vertebrate by-catches and ground beetle (Coleoptera: Carabidae) and spider (Araneae)  
1099 sampling. *Methods Ecol Evol* 2: 185-190.

1100 Spence JR, and Niemelä J (1994) Sampling carabid assemblages with pitfall traps: the  
1101 madness and the method. *Can Entomol* 126: 881–894.

1102 Topping CJ, Sunderland KD (1992) Limitations to the pitfall traps in ecological-sudies  
1103 exemplified by a study of spiders in a field of winter-wheat. *J Appl Ecol* 29: 485–491.

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1109 **Online Resource 3**

1110 Trait data used to describe the functional features of the 110 species recorded in the dataset.

Family	Species	Body	Phenology	Daily activity	Hunting	Substrat
Agelenidae	<i>Coelotes terrestris</i>	13	Spring	Nocturnal	Sheet web	Surface
	<i>Eratigena picta</i>	7	Autumn-Winter	Both	Sheet web	Surface
	<i>Tegenaria silvestris</i>	7	Eurychron	Both	Sheet web	Surface
Amaurobiidae	<i>Amaurobius similis</i>	12	Eurychron	Nocturnal	Sheet web	Surface
Atypidae	<i>Atypus affinis</i>	15	Eurychron	Both	Ambush hunters	Surface
Clubionidae	<i>Clubiona comta</i>	6	Summer	Nocturnal	Other hunters	Vegetation
	<i>Clubiona terrestris</i>	7	Eurychron	Nocturnal	Other hunters	Surface
Dictynidae	<i>Cicurina cicur</i>	7	Eurychron	Both	Ground hunters	Surface
Dysderidae	<i>Dysdera erythrina</i>	10	Eurychron	Nocturnal	Ground hunters	Surface
	<i>Dysdera fuscipes</i>	3.2	Spring	Nocturnal	Ground hunters	Surface
	<i>Harpactea hombergi</i>	7	Eurychron	Nocturnal	Ground hunters	Vegetation
Gnaphosidae	<i>Drassyllus lutetianus</i>	7.5	Spring	Both	Ground hunters	Surface
	<i>Haplodrassus silvestris</i>	10	Summer	Both	Ground hunters	Surface
	<i>Trachyzelotes pedestris</i>	8	Summer	Both	Ground hunters	Surface
	<i>Zelotes apricorum</i>	9	Summer	Both	Ground hunters	Surface
Hahniidae	<i>Hahnia helveola</i>	3	Eurychron	Both	Sheet web	Surface
	<i>Hahnia ononidum</i>	2.5	Autumn-Winter	Both	Sheet web	Surface
	<i>Iberina montana</i>	2	Eurychron	Both	Sheet web	Surface
Linyphiidae	<i>Agneta ramosa</i>	2.5	Summer	Both	Sheet web	Surface
	<i>Bathyphantes gracilis</i>	2.5	Eurychron	Both	Sheet web	Surface
	<i>Centromerus albidus</i>	1.5	Eurychron	Both	Sheet web	Surface
	<i>Centromerus brevipalpus</i>	3	Autumn-Winter	Both	Sheet web	Surface
	<i>Centromerus dilutus</i>	1.5	Eurychron	Both	Sheet web	Surface
	<i>Centromerus serratus</i>	1.7	Eurychron	Both	Sheet web	Surface
	<i>Centromerus sylvaticus</i>	4	Eurychron	Both	Sheet web	Surface
	<i>Ceratinella scabrosa</i>	2.3	Summer	Both	Wandering web	Surface
	<i>Dicymbium tibiale</i>	2.6	Eurychron	Both	Wandering web	Surface
	<i>Diplocephalus cristatus</i>	2.5	Eurychron	Both	Wandering web	Surface
	<i>Diplocephalus latifrons</i>	2	Eurychron	Both	Wandering web	Surface
	<i>Diplocephalus picinus</i>	1	Summer	Both	Wandering web	Surface
	<i>Diplostyla concolor</i>	3	Eurychron	Both	Sheet web	Surface
	<i>Erigone atra</i>	2.8	Eurychron	Both	Wandering web	Surface
	<i>Erigone dentipalpis</i>	2.6	Eurychron	Both	Wandering web	Surface
	<i>Gonatium rubellum</i>	3.4	Eurychron	Both	Wandering web	Surface
	<i>Gongylidiellum latebricola</i>	1.9	Summer	Both	Wandering web	Surface
	<i>Gongylidiellum vivum</i>	1.9	Eurychron	Both	Wandering web	Surface
	<i>Gongylidium rufipes</i>	3.7	Summer	Both	Wandering web	Surface
	<i>Jacksonella falconeri</i>	1.2	Eurychron	Both	Wandering web	Surface
<i>Labulla thoracica</i>	6.4	Eurychron	Both	Sheet web	Vegetation	
<i>Linyphia hortensis</i>	5	Spring	Both	Sheet web	Vegetation	
<i>Macrargus rufus</i>	4.6	Eurychron	Both	Sheet web	Surface	

	<i>Maro minutus</i>	1.5	Eurychron	Both	Sheet web	Surface
	<i>Maso sundevalli</i>	1.8	Eurychron	Both	Wandering web	Vegetation
	<i>Micrargus apertus</i>	2.2	Eurychron	Both	Wandering web	Surface
	<i>Micrargus herbigradus</i>	1.9	Eurychron	Both	Wandering web	Surface
	<i>Microneta viaria</i>	3	Eurychron	Both	Sheet web	Surface
	<i>Minyriolus pusillus</i>	1.3	Spring	Both	Wandering web	Surface
	<i>Monocephalus fuscipes</i>	2.2	Eurychron	Both	Wandering web	Surface
	<i>Neriene clathrata</i>	5	Eurychron	Both	Sheet web	Vegetation
	<i>Oedothorax apicatus</i>	3.3	Eurychron	Both	Wandering web	Surface
	<i>Oedothorax retusus</i>	3	Eurychron	Both	Wandering web	Surface
	<i>Ostearius melanopygius</i>	2.6	Eurychron	Both	Wandering web	Surface
	<i>Palliduphantes pallidus</i>	2.3	Eurychron	Both	Sheet web	Vegetation
	<i>Parapelecopsis nemoralis</i>	2.1	Eurychron	Both	Wandering web	Surface
	<i>Pocadicnemis pumila</i>	2.2	Spring	Both	Wandering web	Surface
	<i>Saaristoa abnormis</i>	4	Eurychron	Both	Sheet web	Surface
	<i>Saloca diceros</i>	1.4	Autumn-Winter	Both	Sheet web	Surface
	<i>Sintula corniger</i>	2	Eurychron	Both	Wandering web	Surface
	<i>Tapinocyba mitis</i>	1.5	Autumn-Winter	Both	Wandering web	Surface
	<i>Tenuiphantes cristatus</i>	2.8	Autumn-Winter	Both	Sheet web	Vegetation
	<i>Tenuiphantes flavipes</i>	2.5	Eurychron	Both	Sheet web	Vegetation
	<i>Tenuiphantes tenuis</i>	3.2	Eurychron	Both	Sheet web	Vegetation
	<i>Tenuiphantes zimmermanni</i>	3.2	Eurychron	Both	Sheet web	Vegetation
	<i>Tiso vagans</i>	2.2	Eurychron	Both	Wandering web	Surface
	<i>Trichoncus affinis</i>	2.5	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria acuminata</i>	4	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria atrotibialis</i>	2.8	Summer	Both	Wandering web	Surface
	<i>Walckenaeria corniculans</i>	3	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria cucullata</i>	2.7	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria cuspidata</i>	2.9	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria dysderoides</i>	2.2	Spring	Both	Wandering web	Surface
	<i>Walckenaeria incisa</i>	3.2	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria mitrata</i>	3.3	Spring	Both	Wandering web	Surface
	<i>Walckenaeria nudipalpis</i>	2.7	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria obtusa</i>	3.8	Eurychron	Both	Wandering web	Surface
	<i>Wiehlea calcarifera</i>	1.3	Eurychron	Both	Wandering web	Surface
Liocranidae	<i>Agroeca brunnea</i>	8	Eurychron	Both	Ground hunters	Surface
	<i>Apostenus fuscus</i>	4	Eurychron	Both	Ground hunters	Surface
	<i>Scotina celans</i>	4.7	Eurychron	Both	Ground hunters	Surface
Lycosidae	<i>Alopecosa pulverulenta</i>	10	Summer	Diurnal	Ground hunters	Surface
	<i>Hygrolycosa rubrofasciata</i>	6	Spring	Diurnal	Ground hunters	Surface
	<i>Pardosa amentata</i>	8	Summer	Diurnal	Ground hunters	Surface
	<i>Pardosa hortensis</i>	5.5	Summer	Diurnal	Ground hunters	Surface
	<i>Pardosa prativaga</i>	6	Summer	Diurnal	Ground hunters	Surface
	<i>Pardosa proxima</i>	6.5	Summer	Diurnal	Ground hunters	Surface
	<i>Pardosa pullata</i>	6	Eurychron	Diurnal	Ground hunters	Surface
	<i>Pardosa saltans</i>	5.7	Summer	Diurnal	Ground hunters	Surface
	<i>Pirata uliginosus</i>	6	Summer	Diurnal	Ground hunters	Surface

	<i>Piratula hygrophila</i>	6.5	Summer	Diurnal	Ground hunters	Surface
	<i>Piratula latitans</i>	5	Summer	Diurnal	Ground hunters	Surface
	<i>Trochosa ruricola</i>	14	Eurychron	Diurnal	Ground hunters	Surface
	<i>Trochosa terricola</i>	14	Eurychron	Diurnal	Ground hunters	Surface
Miturgidae	<i>Zora spinimana</i>	6.5	Eurychron	Both	Ground hunters	Surface
Phrurolithidae	<i>Phrurolithus festivus</i>	3	Summer	Both	Ground hunters	Surface
Salticidae	<i>Neon reticulatus</i>	3	Eurychron	Diurnal	Other hunters	Surface
Tetragnathidae	<i>Metellina mengei</i>	6	Summer	Both	Orb web	Vegetation
	<i>Pachygnatha clercki</i>	7	Eurychron	Both	Orb web	Surface
	<i>Pachygnatha degeeri</i>	3.7	Eurychron	Both	Orb web	Surface
Theridiidae	<i>Enoplognatha thoracica</i>	4	Eurychron	Both	Space web	Surface
	<i>Euryopsis flavomaculata</i>	4	Summer	Both	Space web	Surface
	<i>Pholcomma gibbum</i>	1.5	Eurychron	Both	Space web	Surface
	<i>Robertus lividus</i>	4	Eurychron	Both	Space web	Surface
	<i>Theonoe minutissima</i>	1.2	Eurychron	Both	Space web	Surface
	<i>Theridion mystaceum</i>	2.5	Summer	Both	Space web	Vegetation
Thomisidae	<i>Cozyptila blackwalli</i>	4	Eurychron	Both	Ambush hunters	Surface
	<i>Ozyptila praticola</i>	4	Eurychron	Both	Ambush hunters	Surface
	<i>Ozyptila trux</i>	5	Eurychron	Both	Ambush hunters	Surface
	<i>Xysticus cristatus</i>	8	Summer	Both	Ambush hunters	Vegetation
	<i>Xysticus luctator</i>	10	Summer	Both	Ambush hunters	Surface
Zodariidae	<i>Zodarion italicum</i>	3	Summer	Both	Ambush hunters	Surface

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1124 **Online Resource 4**

1125 Species richness, richness estimator and completeness of each site of the datasets. Completeness is the  
 1126 ratio between observed and estimated richness (Soberón et al., 2007). For each site, completeness was  
 1127 based on three estimators (Chao2, Jacknife 1 and ICE). For species richness and completeness values  
 1128 are means  $\pm$  standard errors.

	No of plots	Total richness	Mean species richness $\pm$ se	Chao2	Jacknife 1	ICE	Completeness index $\pm$ se
Overall datasets	56	110	19.02 $\pm$ 0.75	0.80	0.91	0.79	0.83 $\pm$ 0.04
<u>Recent woodlands</u>	19	71	17.42 $\pm$ 1.12	0.49	0.85	0.70	0.68 $\pm$ 0.11
Coetquidan	6	32	16 $\pm$ 1.15	0.80	0.78	0.91	0.83 $\pm$ 0.04
Kério	6	38	17.33 $\pm$ 1.61	0.73	0.73	0.87	0.78 $\pm$ 0.05
Sal	4	41	23.75 $\pm$ 1.97	0.77	0.73	0.84	0.78 $\pm$ 0.03
Stangala	3	21	12 $\pm$ 0.58	0.63	0.66	0.69	0.66 $\pm$ 0.02
<u>Ancient forests</u>	37	101	19.84 $\pm$ 0.95	0.72	0.87	0.75	0.78 $\pm$ 0.05
Avaugour	6	28	13.33 $\pm$ 1.05	0.86	0.78	0.90	0.85 $\pm$ 0.04
Beumanoir	3	29	19.67 $\pm$ 0.88	0.82	0.75	0.83	0.80 $\pm$ 0.03
Beffou	5	45	21.8 $\pm$ 1.88	0.79	0.74	0.85	0.80 $\pm$ 0.03
Bois du Chap	2	19	-	-	-	-	-
Coat-an-noz	3	32	21.33 $\pm$ 4.33	0.69	0.71	0.80	0.74 $\pm$ 0.03
Corbières	3	37	21.33 $\pm$ 1.33	0.72	0.68	0.72	0.70 $\pm$ 0.01
Cranou	2	46	-	-	-	-	-
Lorges	3	24	16 $\pm$ 0.58	0.78	0.73	0.81	0.77 $\pm$ 0.02
Menez	1	13	-	-	-	-	-
Rennes	3	49	28 $\pm$ 2.65	0.61	0.66	0.69	0.65 $\pm$ 0.02
Soeuvres	2	33	-	-	-	-	-
Tremelin	4	40	22 $\pm$ 3.03	0.87	0.76	0.85	0.83 $\pm$ 0.04

1130 **Online Resource 5**

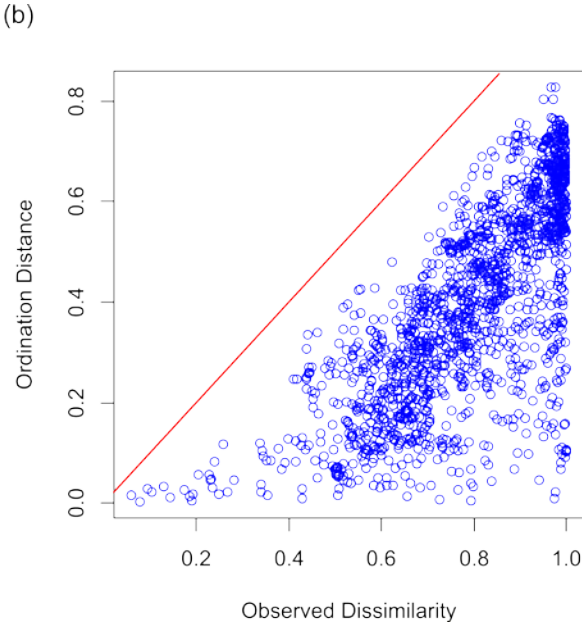
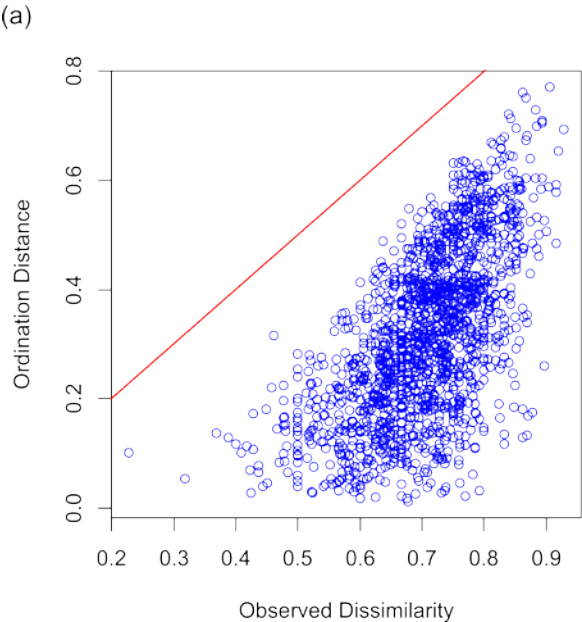
1131 Summary of the statistical tests for all the indices used to analyse differences in structure,  
 1132 taxonomic and functional  $\alpha$ -diversity of spider communities of ancient forests and recent  
 1133 woodlands.

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<b>Metrics</b>	<b>Ancient forests</b>	<b>Recent woodlands</b>	<b>Wald's test</b>	<b><i>p</i></b>
Species richness	19.8 ± 0.95	17.4 ± 1.11	1.4	0.24
Standardised abundance (log)	127.2 ± 13.4	121.3 ± 13.1	0.04	0.85
Pielou' evenness	0.75 ± 0.02	0.77 ± 0.02	0.6	0.44
FRic	0.12 ± 0.01	0.08 ± 0.02	3.12	0.08
FDiv	0.72 ± 0.02	0.74 ± 0.02	0.11	0.73
FR	0.46 ± 0.01	0.47 ± 0.01	0.19	0.66
<i>I<sub>RR</sub></i> (log)	0.30 ± 0.05	0.32 ± 0.06	0.16	0.69
FRar	0.86 ± 0.004	0.85 ± 0.004	1.43	0.23
FOri (log)	0.007 ± 0.001	0.004 ± 0.001	12.9	0.0003
FSpe	0.36 ± 0.01	0.36 ± 0.01	0.4	0.53
CWM <sub>Body</sub>	1.3 ± 0.2	1.19 ± 0.03	6.7	0.01
CWM <sub>Phenology: Autumn/Winter</sub>	0.08 ± 0.01	0.03 ± 0.01	11.4	0.0007
CWM <sub>Phenology: Eurychron</sub>	0.73 ± 0.01	0.74 ± 0.02	1.06	0.30
CWM <sub>Phenology: Spring</sub>	0.03 ± 0.01	0.03 ± 0.01	0.01	0.92
CWM <sub>Phenology: Summer</sub>	0.15 ± 0.01	0.19 ± 0.02	1.56	0.21
CWM <sub>Daily activity: Both</sub>	0.82 ± 0.01	0.88 ± 0.02	3.74	0.05
CWM <sub>Daily activity: Diurnal</sub>	0.09 ± 0.01	0.07 ± 0.01	1.21	0.27
CWM <sub>Daily activity: Nocturnal</sub>	0.09 ± 0.01	0.05 ± 0.01	1.32	0.25
CWM <sub>Guild: Ambush hunters</sub>	0.16 ± 0.004	0.03 ± 0.01	1.39	0.24
CWM <sub>Guild: Ground hunters</sub>	0.19 ± 0.01	0.15 ± 0.02	3.63	0.056
CWM <sub>Guild: Orb web</sub>	0.005 ± 0.002	0.01 ± 0.01	4.34	0.03
CWM <sub>Guild: Others hunters</sub>	0.03 ± 0.01	0.01 ± 0.01	4.75	0.03
CWM <sub>Guild: Sheet web</sub>	0.45 ± 0.02	0.45 ± 0.03	0.09	0.76
CWM <sub>Guild: Space web</sub>	0.04 ± 0.01	0.07 ± 0.01	8.94	0.003
CWM <sub>Guild: Wandering web</sub>	0.28 ± 0.02	0.28 ± 0.01	0.01	0.92
CWM <sub>Stratum: Ground-dwellers</sub>	0.85 ± 0.01	0.8 ± 0.01	16.9	< 0.0001
CWM <sub>Stratum: Vegetation-dwellers</sub>	0.16 ± 0.01	0.2 ± 0.01	16.9	< 0.0001

1135 **Online Resource 6**

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1137 Shepard diagrams showing the goodness of fit of the measured pairwise dissimilarities of the  
1138 spider assemblages as compared to the pairwise dissimilarities represented by PCoA  
1139 ordination, for the taxonomic level (a) and the functional level (b).



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1159 **Online Resource 7**

1160 Table representing the distribution of the 110 spider species between ancient forests and  
 1161 recent woodlands with their weight of functional originality (a) and specialisation (b) assessed  
 1162 from the functional space (see Table 1 for details of metrics). Coloured circles represent  
 1163 abundance standardised based on the number of days a trap was active. Grey circles represent  
 1164 the frequency of the species in each forest category (e.g. 0.25 for ancient forests, i.e. one  
 1165 species observed in 9/37 plots).

